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From Poe to Ponder...and Lindberg: Introduction to the symposium "Molluscs as models in evolutionary biology"*

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Known to students of our profession and concisely summarized most recently in Ponder and Lindberg (2008), Mollusca are, with an estimated 200,000 living species, one of the largest animal phyla, second only to the arthropods. The remarkably rich fossil record of molluscs throws light back into the earliest Cambrian revolution 543 million years ago, and ever since then we find them in nearly every ecosystem on Earth. The classes of living and fossil molluscs comprise an array of diverse animals with the most varied body plans, ranging from minute worm-like animals dwelling between sand grains on the beach to giant squids in the deep sea, and from microscopic snails in leaf-litter to giant clams in coral reefs. As objects of fascination, function, and food, molluscs play important roles in many cultures and societies. They include many taxa of immense economic significance, such as oysters, scallops, and squids; some bivalves produce precious pearls, and some snails carry diseases that infect millions of people, especially in the tropics.

Yet we feel that it is not only a curious fact in the history of science, but, unfortunately enough, much more a symptomatic indication of our discipline that it was not a professional naturalist or scientist with an interest in malacology, but the poet Edgar Allen Poe (1809-1849), who formulated an idea with much future. Poe was among the first to recognize and explicitly recommend that the study of molluscs requires a combined analysis, which in his times meant reconciling a classification based on hard shells with evidence from soft body anatomy (see details on this in the opening remarks to the symposium by Glaubrecht (2009)). This synthetic idea was long ignored by conchologists, who continued to classify molluscs almost exclusively based on features of their shell, while neglecting the soft body and the biological information that it holds. As a consequence, for a long time we knew few hard facts, for example, about the evolution and phylogeny of these soft-bodied animals but instead had much speculation by self-proclaimed authorities in the field.

In addition, most contributions in malacology long centered around morphology, anatomy, and in particular phylogenetic relationships within and among constituent taxa. Only rarely have molluscs been utilized explicitly as models for the study of the general aspects of evolutionary biology. However, molluscs, with their many features and facets, are highly suitable for providing some fundamental insights into the mechanisms of the genesis of biodiversity, its pattern in historical biogeography, and the underlying processes of speciation and radiation. An increasing number of recent studies and publications on molluscs reveal this rich potential.

Therefore, it was the aim of this symposium on molluscs as models in evolutionary biology, held during the World Congress of Malacology (WCM) in Antwerp from the 15th to 20th July 2007 (jointly organized by Unitas Malacologia and the American Malacological Society), to bring together experts and their expertise to provide—based on molluscs—some of those fundamental studies, and to show avenues for using data that are of relevance for evolutionary biology. With 43 talks over more than two full days of sessions (plus several posters), this symposium was the largest at the Antwerp WCM. Following the introduction, two invited keynotes or plenary lectures were given, one by Suzanne Williams and David Reid (on global pattern of diversity and speciation) and one by Thomas Wilke and Christian Albrecht (on genesis of biodiversity, focusing on ancient lakes). Other lectures covered a wide array of topics ranging from biogeography, shell morphology and evolution, molecular phylogenetics, radiations and extinctions as documented in the fossil record, to mitogenomics, and aspects of development and reproduction. From all these presentations, a selection of eleven contributions were made, and we invited the authors to work out their main subject as exemplars for their specific area of research, viewed from their individual perspective. Subsequently, eight of the original speakers have been able to provide manuscripts for the *American Malacological Bulletin*.

* From the symposium "Molluscs as models in evolutionary biology: from local speciation to global radiation" presented at the World Congress of Malacology, held from 15 to 20 July 2007 in Antwerp, Belgium.

Three other papers of those originally invited have been published elsewhere in the meantime, viz. Lindberg (2007) on a case study from the limpet *Scutellastra flexuosa* (Quoy and Gaimard, 1834) from Moorea, contrasting the respective roles of deep phylogenetic history with recent adaptations in shaping current ecological and life history characteristics, Hershler and Liu (2008) on vicariance and dispersal of hydrobiid springsnails in the southwestern United States, and Williams and Duda (2008) on biogeography and speciation.

We feel that together with these papers, the studies presented here dealing with phenomena from local speciation to global radiations, and including both the paleontological as well as neonotological perspective, underline the potential that molluscs have as models in evolutionary biology. The first contribution by Wilke *et al.* ("As time goes by...") provides a concise review of molecular clock methods and is at the same time a hands-on manual for molecular clock analyses. This contribution specifically is aimed at researchers in malacology, giving external clock rates for the cytochrome oxidase subunit I which may be applied for most aquatic molluscan taxa and even other invertebrates. Molecular clocks have become a standard tool in evolutionary biology and this review provides a sound basis for extending the use of molluscs as models. The next two papers by Hayes *et al.* on "Apple snails as a system for addressing fundamental questions" and by Holland and Cowie on "Land snail models in island biogeography" exemplarily highlight the use of taxa like freshwater and terrestrial gastropods for addressing major issues in evolutionary research. A common focus of both studies is on exploring patterns of biogeography, and in particular island colonization for the Hawaiian Succineidae and Achatinellinae. In addition, Hayes *et al.* also discuss the role of ampullariids in advancing knowledge of speciation and adaptation processes. Subsequently, Elejalde *et al.* (on the "land snail genus *Pyrenaearia*") uses these Iberian helicids to investigate the link between molecular data (DNA taxonomy) and classic taxonomy on one hand, and the role of climate in diversification on the other hand. While all papers so far rely heavily on molecular data, the last three papers in this symposium cover other important aspects of molluscs also relevant in evolutionary biology. Wesselingh and Renema ("Molluscan evolution from ancient long-lived lakes") offer a paleontological perspective on snail diversification in Miocene Amazonian Lake Pebas. Their focus is on the tempo and mode of evolutionary change in what we like to term a 'natural laboratory', as it has model characteristics also for interpreting evidence from modern long-lived lakes. The paper by Sigwart on "cladistic analysis in Polyplacophora" again focuses on a recent group, the living chitons, and aims at elucidating the role and value of morphological characters in tracking the phylogenetic relationships and evolution. In a nutshell, this paper questions the value of morphological characters in a molecular world. The final contribution, by Smirthwaite *et al.* on "the use of developmental sequences", offers a glimpse of molluscs in developmental biology, which is a renaissance issue in evolutionary research. Using freshwater pulmonates, the authors discuss the potential of molluscs to offer mechanistic explanations of ontogeny, including heterochrony.

We hope that these studies and the avenues they suggest will further facilitate the influence of malacology within evolutionary biology, even more so in the future than it was the case in the past. It is a pleasure to thank all who participated in this symposium during the Antwerp WCM meeting and, in particular, the speakers who contributed to what we felt to be a stimulating session, as reflected in the many discussions. We are most grateful to the authors that have contributed to this symposium volume and to Ken Brown, who kindly offered to publish these contributions as an outcome of the symposium. Finally, we would also like to thank Thierry Backeljau from the Royal Belgian Institute of Natural Sciences in Brussels, and at that time president of Unitas Malacologica, for inviting us (shortly after the Perth meeting in 2004) and then helping to organize this symposium in 2007.

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